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Statement of authorship

MJ, BEM and SC designed the study. MJ performed the literature collection, data extraction and analysis, and wrote the initial manuscript, with significant input from BEM. SC, HZ, KF, KYC, and

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Abstract

Phosphorus (P) is an essential macro-nutrient required for plant metabolism and growth. Low P availability could potentially limit plant responses to elevated carbon dioxide (eCO_2), but consensus has yet to be reached on the extent of this limitation. Here, based on data from experiments that manipulated both CO_2 and P for young individuals of woody and non-woody species, we present a meta-analysis of P limitation impacts on plant growth, physiological, and morphological response to eCO_2. We show that low P availability attenuated plant photosynthetic response to eCO_2 by approximately one-quarter, leading to a reduced, but still positive photosynthetic response to eCO_2 compared to those under high P availability. Furthermore, low P limited plant aboveground, belowground and total biomass responses to eCO_2, by 14.7%, 14.3% and 12.4%, respectively, equivalent to an approximate halving of the eCO_2 responses observed under high P availability. In comparison, low P availability did not significantly alter the eCO_2-induced changes in plant tissue nutrient concentration, suggesting tissue nutrient flexibility is an important mechanism allowing biomass response to eCO_2 under low P availability. Low P significantly reduced the eCO_2-induced increase in leaf area by 14.3%, mirroring the aboveground biomass response, but low P did not affect the eCO_2-induced increase in root length. Woody plants exhibited stronger attenuation effect of low P on aboveground biomass response to eCO_2 than non-woody plants, whilst plants with different mycorrhizal associations showed similar responses to low P and eCO_2 interaction. This meta-analysis highlights crucial data gaps in capturing plant responses to eCO_2 and low P availability. Field-based experiments with longer-term exposure of both CO_2 and P manipulations are critically needed to provide ecosystem-scale understanding. Taken together, our results provide a quantitative baseline to constrain model-based hypotheses of plant responses to eCO_2 under P limitation, thereby improving projections of future global change impacts.

Keywords: soil phosphorus, carbon dioxide, meta-analysis, biomass, leaf gas exchange, nutrient concentration, plant morphology, plant nutrient uptake, mycorrhizae

Introduction

The anthropogenic increase in atmospheric carbon dioxide (CO_2) directly affects plant physiology, tissue chemical composition, morphology, and biomass, but the dependence of these responses on plant-available soil phosphorus (P) remains uncertain (Achat, Augusto, Gallet-Budynek and Loustau, 2016; Curtis and Wang, 1998; Huang, Houlton, Marklein, Liu and Zhou, 2015; Jiang, Caldararu, Zaehle, Ellsworth and Medlyn, 2019a; Jin, Tang and Sale, 2015; Norby et al., 2016; Norby and Zak, 2011; Reed, Yang and Thornton, 2015). With about one-third of the world's soils estimated to be low in P availability (Cleveland et al., 2011; Goll et al., 2012; Reich and Oleksyn, 2004; Yang and Post, 2011), plant P limitation is observed in many terrestrial ecosystems, not restricted to tropical ecosystems (Crous, Osvaldsson and Ellsworth, 2015; Lang et al. 2017; Vitousek and Howarth, 1991; Wright et al., 2018; Hou et al., 2020). As anthropogenic nitrogen (N) deposition increases N availability, the influence of P availability on plants is likely to increase in many regions in the future due to the induced N:P imbalances, including in ecosystems on younger soils not currently considered to be P-limited (Jonard et al. 2015; Peñuelas et al. 2013). While there is an extensive pool of experimental literature on plant responses to elevated CO_2 (eCO_2) (Ainsworth and Long, 2005; Curtis and Wang, 1998; Ellsworth et al., 2012; Jin et al., 2015) and P fertilization independently (Crous et al., 2015; Hawkesford et al., 2012; J. Jiang et al., 2019; Tian et al., 2019), there is a lack of understanding of the interaction between low P and eCO_2 (M. Jiang et al., 2019a). Given the widespread low P availability in global terrestrial ecosystems (Norby et al., 2016), improving understanding of the interactive effect of soil P availability and eCO_2 is fundamental to the prediction of terrestrial ecosystem responses to climate change (Huang et al., 2015; Zhang, Pitman, Wang, Dai and Lawrence, 2013; Zhang, Wang, Matear, Pitman and Dai, 2014).

The importance of plant P supply for global carbon-climate feedbacks has led to an increase in the number of land surface models that incorporate P cycle processes (CNP models; Goll et al., 2012; Wang, Houlton and Field, 2007; Yang, Thornton, Ricciuto and Post, 2014; Thum et al., 2019; Zhu et al., 2019). However, different models implement different representations of the P cycle and its effect on plant processes, leading to diverging predictions of plant responses to eCO_2 (Fleischer et al., 2019;

Medlyn et al., 2016). For example, one version of the Community Land Model (CLM) assumes fixed tissue nutrient concentrations (Yang et al., 2014). It predicts a strong photosynthetic response to eCO_2 if P is not limiting, but downregulates this response under low P supply because tissue stoichiometry is assumed to be fixed and little additional P uptake is stimulated to match the additional carbon (Medlyn et al., 2016). The Community Atmosphere-Biosphere Land Exchange model (CABLE) also predicts a strong eCO_2 effect on growth if P is abundant, but it assumes that plants increase their autotrophic respiration rather than downregulate photosynthesis to limit the biomass response to eCO_2 under low P supply (Medlyn et al., 2016; Wang et al., 2007; but see Crous et al. 2017). Other models, such as ELM-ECA, assume that eCO_2 may stimulate plant P acquisition via increased biochemical mineralization, which in turn, may partially alleviate plant P stress and therefore sustain a positive growth response to eCO_2 in low P soils (Fleischer et al., 2019; Zhu, Riley, Tang and Koven, 2016). The diverse range of model assumptions and the different mechanisms that they describe suggest a prognostic knowledge gap on how P availability affects plant responses to eCO_2, highlighting the need for a quantitative synthesis of the available experimental data to better constrain model projections. The key questions that should be addressed by such a synthesis are: (1) to what extent does P limitation modulate the response of plant photosynthesis and biomass to eCO_2? (2) to what extent do changes in plant tissue stoichiometry and nutrient uptake enable a biomass response to eCO_2 under low P? and (3) do these responses differ by plant forms and/or symbiotic associations?

Quantification of P limitation effects on plant responses to eCO_2 can be achieved by controlled multi-factorial experiments manipulating P availability and atmospheric CO_2 concentration at the same time. Low P supply in these experiments is generally considered to be a stressed condition to the experimental plants. A diversity of responses has been observed in these experiments. Some P x CO_2 studies find that P-limited vegetation growth is not strongly, if at all, stimulated by eCO_2 (Edwards, McCaffery and Evans, 2005; Jin, Tang, Armstrong and Sale, 2012; Lam, Chen, Norton and Armstrong, 2012; Singh, Reddy, Fleisher and Timlin, 2014; Stöcklin and Körner, 1999). As a corollary, plant tissue P concentrations may be less responsive to eCO_2 in low P compared to high P treatment, because there is less additional carbon (C) uptake under eCO_2 and therefore less nutrient dilution (Conroy et al. 1990; Gifford, Barrett and Lutze, 2000; Lloyd, Bird, Veenendaal and Kruijt,

2001; Norby, O'Neill and Luxmoore, 1986). However, other studies have shown that eCO_2 can increase growth even in low P soils (Imai and Adachi, 1996; Newbery, Wolfenden, Mansfield and Harrison, 1995; Pandey et al., 2015), because plants can grow more efficiently via an increased C:P ratio, or via allocation of the additional carbon fixed under eCO_2 to enhance soil P acquisition (Keith et al., 1997; Körner, 2006; Norby, Cotrufo, Ineson, O'Neill and Canadell, 2001). Given the diversity of responses, a meta-analysis is crucially needed to synthesize P x CO_2 experiments and identify the general process-based patterns.

The magnitude and direction of the net response to P and CO_2 manipulation may depend on the supply rate, the strength or the duration of the treatment perturbation, as well as the plant growth form and/or symbiotic associations. Plants of different growth forms (e.g. woody vs. non-woody) have been shown to respond differently to rising CO_2 (Saxe, Ellsworth and Heath, 1998; Ainsworth and Long, 2004; Ainsworth and Rogers, 2007). There is a large body of literature showing that woody plants with longer lifespan and larger investment in stem biomass are more responsive to eCO_2 than non-woody herbaceous plants (Saxe, Ellsworth and Heath, 1998; Ainsworth and Long, 2004; Ainsworth and Rogers, 2007). This larger response of woody plants may be due to the positive growth feedbacks inherent in trees that allow them to grow exponentially (Norby and Zak, 2011; Kirschbaum and Lambie; 2015; Norby et al. 2016). Similarly, it has been suggested that mycorrhizal association is a crucial factor modulating plant responses to eCO_2 and its interaction with nutrient availability (Treseder, 2004; Terrer, Vicca, Hungate, Phillips, and Prentice, 2016; Terrer et al., 2017; Terrer et al., 2019). In particular, empirical relationships showed that, the eCO_2 response of arbuscular mycorrhizal plants was best predicted by soil N availability (Terrer et al., 2016), whilst the eCO_2 response of ectomycorrhizal plants was best predicted by soil P availability (Terrer et al., 2019). These differences in mycorrhizal effect on plant responses to eCO_2 were thought to be related to how different nutrients were acquired, processed and allocated to plants by their symbiotic mycorrhizal fungi (Van der Heijden, Martin, Sellose and Sanders, 2015; Terrer et al., 2017; Terrer et al., 2019). A meta-analysis of the dependency of P x CO_2 interaction effect on different plant groups and mycorrhizal associations would allow for more robust empirical relationships and therefore higher predictive capacity.

With the aim of providing guidance to improve model predictions of plant responses to eCO_2 under low P availability and identifying priorities for future experiments, we compiled data collected from P by CO_2 multi-factorial experiments, and performed a meta-analysis. We extracted the individual and interactive effects of P and CO_2 treatments on gas exchange, plant biomass, tissue nutrient concentration, morphology, nutrient uptake capacity, and resource use efficiency. We considered ambient CO_2 (aCO_2) and high P (HP) supply as the baseline treatments, and eCO_2 and low P supply (LP) as the experimental treatments (more details in the methods section). Our consideration of HP as control and LP as treatment reflects both experimental design – where there are several levels of P addition in an experiment, levels include several LP treatments and one HP treatment (Figure S2) – and model development history, since new models, in which P cycle processes have been added, are being now compared to previous CN models which implicitly assume high P availability (Fleischer et al., 2019). We evaluated the effects of P availability on plant responses to eCO_2, by hypothesizing that: **H1)** the eCO_2-induced increase in photosynthesis would be reduced by LP treatment; **H2)** the eCO_2-induced increase in plant biomass would be reduced by LP treatment, with the reduction being stronger for the aboveground biomass response than the belowground biomass; **H3)** eCO_2 would reduce plant tissue nutrient concentration, but the magnitude of reduction would be smaller under LP treatment; **H4)** woody plant responses to eCO_2 would be more strongly affected by LP treatment than those of non-woody plants; and **H5)** plants with ectomycorrhizal association would show a stronger eCO_2 x P interaction than plants with arbuscular mycorrhizae. Hypotheses H1 – H4 are generally consistent with process representations in existing terrestrial biosphere models (Fleischer et al., 2019; Medlyn et al., 2016), whilst H5 has recently been shown to be an important mechanism in modulating plant responses to eCO_2 (Terrer et al., 2019). As such, our assessment of these hypotheses represents a timely and important endeavor to improve predictions of terrestrial carbon-phosphorus cycle feedbacks under climate change.

Materials and Methods

Literature search

We compiled literature on P by CO_2 interactions by searching Web of Science using word combinations of "phosphorus" + "CO_2 enrichment" + "plant response", which resulted in a total of 180 papers. An overview of the literature selection and quality check criteria is available in Table S1 and Figure S1. We included original studies that investigated plant responses to both CO_2 and P treatments, which resulted in a total of 45 studies (n_s) on P and CO_2 manipulative experiments (Ref S1), with n_s = 13 on woody (including 5 pine species, and all are seedlings), and n_s = 32 on non-woody plants. The dataset included a total of 59 species, with 18 classified as woody plants. A complete species list is provided in Table S2. All studies included in our analysis used plants growing in pots, including those conducted under field environmental conditions. All studies manipulated soil P availability with P addition, which may alter soil chemical properties beyond P availability (e.g. pH, cation exchange capacity). Here we only focused on the phosphorus effect because not all studies reported changes in soil chemical properties other than phosphorus availability. We extracted response variables in several categories: biomass, tissue nutrient concentration, and nutrient content of major plant organs, including leaf, stem, root; leaf gas exchange, which included leaf-scale CO_2 assimilation rate (A), stomatal conductance (g_s), and intrinsic water-use efficiency ($iWUE = A/g_s$); morphology, which included leaf area (LA), leaf mass per area (LMA), and root length (RL); plant nutrient uptake capacity, which included plant N uptake capacity (N_{upt}) and plant P uptake capacity (P_{upt}); and resource-use efficiency, which included plant nitrogen use efficiency (NUE), and plant phosphorus use efficiency (PUE). Plant nutrient uptake was defined as the amount of nutrients taken up per root mass or per root length over the experimental duration. Plant nutrient-use efficiency was defined as the amount of nutrients in the plant divided by the total biomass at the time of harvest.

We extracted raw data points, including means and uncertainties, from figures using Plot Digitizer V2.6.8 (http://plotdigitizer.sourceforge.net/). Most studies reported uncertainty as one standard error of the mean, but for studies where no information was available as to what error bars represent, we assumed that the reported uncertainty was one standard error. For studies where no error bars were available, we took the standard error to be the aggregated standard error across all studies for the same response variable. Information on plant age, pot size, pot volume and depth, P application frequency and intensity, soil weight and bulk density, and sample size were also collected wherever possible.

We did not include treatment effects of other forcing variables (e.g. nitrogen or water) in this analysis. Our preliminary selection criteria resulted in a total of 1519 valid data entries (n_e) for all variables listed above. We removed duplicated data entries by only including data collected over the longest experimental duration for each study, species and response variable. Our final dataset included a total n_e of 1202, with n_e = 372 for woody plants and 830 for non-woody plants (Figure 1). The median experimental duration in these experiments was 69 days, with a mean experimental duration of 110 days (i.e. mostly exposing plants to experimental manipulation during the growing season).

In our dataset, ambient CO_2 treatment (termed aCO_2 hereafter) ranges from 315 to 400 ppm, and eCO_2 ranges from 514 to 1500 ppm (Table 1; Figure S2). CO_2 exposure was either in growth cabinets, glasshouse, outdoor chambers, or free-air enrichment (n_s = 5), but all plants were restricted to containers. We categorized the P fertilization treatments into high P (HP) and low P (LP) treatments only, with the LP treatment representing a P-deprived condition for plants in most of the experiments (Figure 2). For studies where multiple P fertilization treatments were available, we considered the highest P fertilization treatment as the HP treatment, and considered all else as the LP treatment. Our dataset therefore has repeated data entries from a single study/experiment, and corresponding multiple LP treatments (if any) with the same HP treatment. To account for non-independence, study was a random factor in mixed-model analysis (see below). We tried to incorporate baseline soil available P on top of the P treatment wherever possible, but found that many studies did not provide this information. Some studies also considered zero P addition as the LP treatment, and because some of them did not report baseline soil P condition, the calculated LP to HP ratio (an indicator of the degree of P stress) can be zero (noted in the forest plots in Data Tables S1-S34).

Statistical analysis

We performed statistical analysis on the P by CO_2 interaction response using the R package "*metafor*" (Viechtbauer, 2010). We considered aCO_2 and HP treatment as the baseline treatment, and eCO_2 and LP treatment as the experimental treatment. We calculated the individual response ratios to P and CO_2 manipulation (r_p and r_c, respectively), following:

$$r_p^{aCO_2} = \frac{\overline{X}_{C_aP_l}}{\overline{X}_{C_aP_h}} \text{ under aCO}_2 \text{ treatment;} \quad \text{Eq. 1}$$

$$r_p^{eCO_2} = \frac{\overline{X}_{C_aP_l}}{\overline{X}_{C_aP_h}} \text{ under eCO}_2 \text{ treatment;} \quad \text{Eq. 2}$$

$$r_c^{hP} = \frac{\overline{X}_{C_eP_h}}{\overline{X}_{C_aP_h}} \text{ under high P treatment;} \quad \text{Eq. 3}$$

$$r_c^{lP} = \frac{\overline{X}_{C_eP_l}}{\overline{X}_{C_aP_l}} \text{ under low P treatment} \quad \text{Eq. 4}$$

where $\overline{X}$ represents the mean, C_e and C_a represent eCO_2 and aCO_2 treatments, and P_h and P_l represent HP and LP treatments, respectively. Following Baig, Medlyn, Mercado and Zaehle (2015), we calculated the LP and eCO_2 interaction response ratio (r), which can be understood as the effect of LP on the eCO_2 responses, as:

$$r = \frac{\frac{\overline{X}_{C_eP_l}}{\overline{X}_{C_aP_l}}}{\frac{\overline{X}_{C_eP_h}}{\overline{X}_{C_aP_h}}} \quad \text{Eq. 5}$$

which can be linearized as:

$$\ln(r) = \ln\left(\frac{\overline{X}_{C_eP_l}}{\overline{X}_{C_aP_l}}\right) - \ln\left(\frac{\overline{X}_{C_eP_h}}{\overline{X}_{C_aP_h}}\right) \quad \text{Eq. 6}$$

Based on the additive property of variance (Baig et al., 2015; Hedges, Gurevitch and Curtis, 1999), the variance of the P by CO_2 interaction (v) response ratio was calculated as:

$$v = \frac{SD^2_{C_eP_l}}{n_{C_eP_l}\overline{X}^2_{C_eP_l}} + \frac{SD^2_{C_aP_l}}{n_{C_aP_l}\overline{X}^2_{C_aP_l}} + \frac{SD^2_{C_eP_h}}{n_{C_eP_h}\overline{X}^2_{C_eP_h}} + \frac{SD^2_{C_aP_h}}{n_{C_aP_h}\overline{X}^2_{C_aP_h}} \quad \text{Eq. 7}$$

We then used the function *rma.mv* from the "*metafor*" package to construct a multivariate linear mixed-effects model to estimate the mean and the 95% confidence interval (CI) of the log-transformed response ratios for each individual variable, weighted by the variance of individual studies. In the model, we considered study as a random factor to weight the within-study variation.

Additionally, for the P x CO_2 interaction effect and the P treatment effect estimates, we considered the LP/HP ratio as a moderator in our mixed-effects model. We then normalized all P x CO_2 interaction responses and P treatment responses to a LP/HP ratio of 0.2, which is the mean and median ratio in our dataset (Figure S2). For plant tissue N:P ratios, we generally found no information on variance, and therefore used the inverse of sample size (i.e. $1/n_e$) as a proxy for variance to weight the relative contribution of individual study to the variable average (Hartung, Knapp and Sinha, 2008). For plotting purposes, we back-transformed the log-transformed response ratio and reported the response ratio in the unit of %. We did not consider pot size, climate or other experimental factors (e.g. soil type and pot volume) in our model due to the sporadic availability of such information among studies. We then plotted funnel plots and performed leave-one-out analysis to check possible publication bias and data quality in all major response variables (Figure S3 – S8). Our results suggest that most of the response variables have relatively good data quality and are relatively independent of the influence of outliers.

For key response variables where sufficient data were available, we reported the woody and non-woody plant responses separately. We tested the between-group heterogeneity (Q_M) between woody and non-woody plant responses. A *p*-value of < 0.05 for the Q_M term indicates a statistically significant vegetation type effect. We also tested the effect of mycorrhizal association in modulating plant responses to eCO_2 under P limitation. We used the mycorrhizal database developed by Soudzilovskaia, Vaessen, Barcelo, He, Rahimlou et al. (2020) to link vegetation type with mycorrhizal type. In our dataset, plant species were categorized into the following mycorrhizal status: ectomycorrhizae (ECM), arbuscular mycorrhizae (AM), ericoid mycorrhizae (ERM), non-mycorrhizae (NM), NM+AM, and ECM+AM (Table S2). To perform between-group heterogeneity test of AM vs. ECM, we excluded plant species with ERM and NM classifications (3 species), and categorized plant species that form associations with both ECM and AM fungi as ECM (3 species), following Terrer et al. (2019).

Results

Overview of data availability and quality

Of the 45 studies and ~1200 valid data points synthesized in this study, sample sizes were for different response variables, vegetation types, mycorrhizal associations, and from contributing research groups (Figure 1). Plant biomass was the most investigated response variable, accounting for about half of the data points, followed by plant tissue nutrient concentration, gas exchange, morphology, nutrient ratio, nutrient uptake capacity, and resource use efficiency variables (Figure 1a). About two thirds of the data points were based on non-woody vegetation (Figure 1b). In terms of mycorrhizal associations, all non-woody vegetation synthesized in this study was categorized as AM-plants, whilst woody vegetation included both ECM and AM associations (Figure 1b).

The eCO_2 treatment generally reduced plant tissue nutrient concentrations, whilst the LP treatment typically imposed P limitation to the plants (Figure 2). For studies that reported both leaf N and P concentrations, eCO_2 treatment generally reduced both leaf N and P concentrations, regardless of vegetation types and P treatments (Figure 2a & 2b). For plants grown under HP treatment, most of the data points are above the N:P ratio line of 1:16 (generally considered as a threshold for P limitation; Güsewell, 2004; Ellsworth et al., 2017), indicating no apparent P limitation to the plant (Figure 2a). In comparison, plants grown in LP availability generally had N:P ratios below the 1:20 line, suggesting likely P limitation to the plant (Figure 2b).

Plant gas exchange responses

For all plants combined, we found that LP treatment generally reduced plant photosynthesis (A) (Figure 3a) whilst eCO_2 generally increased it (Figure 3b), with eCO_2-induced stimulation of A higher under HP than LP treatment (21.3 ± 7.3% vs. 17.2 ± 7.0%). Normalizing the response to a LP/HP ratio of 0.2 (the mean and median ratio in our dataset, as per Methods), there was an interaction between eCO_2 and LP such that the stimulation of A by eCO_2 was 7.5% less (or about one-quarter reduction) at LP than HP (Figure 3c). In comparison, stomatal conductance (g_s) was reduced by LP and eCO_2, with a trend towards a stronger eCO_2 effect in LP. Intrinsic water-use efficiency ($iWUE$) was reduced by LP and increased by eCO_2, with a trend towards a smaller eCO_2 response in LP. The interactions of LP and eCO_2 on g_s and $iWUE$ were statistically non-significant, possibly owing to their high response variability and the relatively small sample size.

Plant biomass responses

In terms of biomass response, evidence was consistent and clear that plant biomass responses to eCO_2 were strongly modulated by LP treatment (Figure 4). LP treatment reduced plant aboveground, belowground and total biomass regardless of the CO_2 treatment (Figure 4a), whilst eCO_2 increased plant biomass and more so under HP than LP treatment (Figure 4b). Under a LP/HP ratio of 0.2 (see Methods), the eCO_2-induced increases in plant aboveground, belowground, and total biomass were significantly reduced by LP treatment, by 14.7%, 14.3% and 12.4%, respectively (Figure 4c), equivalent to about halving the eCO_2 stimulation of plant biomass under HP treatment. Notably, the extent to which LP affected plant responses to eCO_2 was similar for aboveground and belowground biomass.

Plant morphological responses

Plant morphological variables also responded to P and CO_2 manipulations, but there were aboveground and belowground differences (Figure 5). The LP treatment reduced total leaf area (*LA*) and increased leaf mass per area (*LMA*) regardless of the CO_2 treatment, but there were no significant root length (*RL*) responses to LP treatment (Figure 5a). In comparison, eCO_2 generally increased *LA, LMA* and *RL,* although some increases were statistically non-significant (Figure 5b). The eCO_2-induced increase in *LA* was significantly reduced by LP by 14.3% (Figure 5c), mirroring the aboveground biomass response observed earlier (Figure 4c). In contrast, *RL* response to eCO_2 was not significantly affected by the LP treatment, suggesting possible asynchronous responses of root biomass and morphology to eCO_2 and LP interactions (Figure 5c).

Plant nutrient cycle responses

Tissue nutrient concentrations were affected by P and CO_2 treatments, but there were no significant interaction effects (Figure 6). The LP treatment consistently reduced plant tissue P concentrations but generally had no effect on plant N concentrations (Figure 6a & d). In comparison, eCO_2 generally reduced plant tissue P and N concentrations, with a tendency for the eCO_2-induced reductions in plant tissue nutrient concentrations to be larger under HP than LP treatment (Figure 6b & e). However,

when normalized to a 0.2 LP/HP ratio (see Methods), there were no statistically significant LP by eCO_2 interaction effects for any tissue nutrient concentration responses (Figure 6c & f), suggesting that the degree of the eCO_2-induced tissue nutrient dilution effect was similar in LP and HP treatments.

Nutrient uptake capacity, calculated as total N and P uptake per unit root biomass or root length (N_{upt} and P_{upt}, respectively), exhibited similar responses to P and CO_2 manipulations (Figure 7). Regardless of the CO_2 treatment, LP reduced N_{upt} and P_{upt} (Figure 7a). In comparison, N_{upt} and P_{upt} did not exhibit significant responses to eCO_2 under either LP or HP treatment (Figure 7b). There were no statistically significant LP by eCO_2 interaction effects on N_{upt} and P_{upt} (Figure 7c).

Effects of growth form and mycorrhizal associations

Finally, we tested for between-group heterogeneity in the responses and found that there were some vegetation-specific plant responses to P by eCO_2 interactions (Table 2; Figure 8). In particular, aboveground biomass and leaf N concentration of woody and non-woody vegetation responded differently: the eCO_2-induced increase in aboveground biomass of woody vegetation was more strongly reduced by LP treatment than that of non-woody vegetation (Figure 8a, b & c; Table 2), and the eCO_2-induced change in leaf N concentration was more negatively affected by LP treatment than that of non-woody vegetation (Figure 8d, e, &f; Table 2). In comparison, woody and non-woody plants showed no statistically significant differences in their interaction effects of LP and eCO_2 on *A, LA, RL,* belowground biomass, total biomass, leaf N and P concentration, and root N and P concentration for woody and non-woody plants (Table 2).

We further tested whether plant responses to P by CO_2 interaction differed between AM- and ECM-plants (Table S3). We found that mycorrhizal association was not a significant predictor for plant biomass, gas exchange, morphological, and tissue nutrient concentration responses to LP and eCO_2 interaction (Table S3; Figure 9a). For AM-plants, we tested whether plant biomass responses to P by CO_2 interaction differed between vegetation types, and showed that the attenuation effect of LP on aboveground biomass response to eCO_2 of woody plants was statistically stronger than that of non-

woody plants (p=0.02; Figure 9b; Table S4). For woody plants, which included both ECM and AM associations, we found that mycorrhizal type was not a statistically significant predictor for aboveground biomass response (Figure 9c; Table S5).

Discussion

Assessment of hypotheses and modeling implications

Our meta-analysis demonstrates how plant responses to eCO_2 are modulated by P availability. We found evidence to support our H1 hypothesis that the eCO_2-induced increase in photosynthesis would be attenuated by LP treatment (Figure 3c), in that LP supply led to a reduced, albeit still positive, photosynthetic response to eCO_2 (Figure 3b). We also found evidence to support our H2 hypothesis that the eCO_2-induced increase in plant biomass would be dampened by LP treatment (Figure 4c), but we did not observe a significant difference between aboveground and belowground biomass responses in this regard (Figure 4b). In fact, all biomass responses to eCO_2 showed similar magnitude of P limitation effect (Figure 4c). The *LA* response to eCO_2 mirrored the aboveground biomass response (Figure 5c). However, the *RL* response to eCO_2 did not correspond to the belowground biomass response, in that the positive *RL* response to eCO_2 at HP was not reduced in LP treatment (Figure 5c). We did not find evidence to support our H3 hypothesis that plant tissue nutrient concentrations would respond less strongly to eCO_2 when exposed to LP treatment (Figure 6). There were also no significant eCO_2 and LP interaction effects on either plant N_{upt} or P_{upt} (Figure 7), which may partly explain the lack of interaction effect on tissue nutrient concentrations. Finally, our between-group heterogeneity tests provided partial evidence to support our H4 hypothesis that woody plant aboveground biomass responses to eCO_2 would be more strongly modulated by LP treatment than those of non-woody plants (Figure 8; Table 2). In comparison, our between-group heterogeneity tests for mycorrhizal effect did not support the H5 hypothesis that mycorrhizal association would be a significant predictor for plant responses to eCO_2 under LP treatment (Figure 9; Table S3, S4 & S5).

In our meta-analysis, *A* was positively stimulated by eCO_2 despite an attenuating effect of LP (Figure 3), suggesting that plants subject to LP retain the capacity to acquire extra carbon under eCO_2. This result is in line with the biochemical evidence that photosynthesis may be maintained under P

deficiency via a faster turnover of the inorganic P pool in leaves, and/or a finely tuned homeostasis of inorganic P in the cytosol and chloroplasts (Ellsworth, Crous, Lambers and Cooke, 2015; Hawkesford et al., 2012; Thomas, Montagu and Conroy, 2006). However, this result contradicts models that assume that photosynthesis is strongly down-regulated in response to eCO_2 when P is limiting (Medlyn et al., 2016; Fleischer et al., 2019). It is possible that without homeostasis, there would be larger P deficiency and downregulation than is observed, which reconciles these observations and model results.

For plant biomass, the meta-analysis results were overall comparable to a recent multi-model intercomparison. Fleischer et al. (2019) carried out a comprehensive assessment of CNP model performance in a P-deprived mature forest ecosystem. The model ensemble predicted that low P availability would strongly constrain the future plant biomass response to eCO_2, by about 50% on average when compared to predictions without P cycle processes (Fleischer et al., 2019). Our results firmly supported this model ensemble prediction, in that the LP treatment consistently reduced the aboveground and belowground biomass responses to eCO_2 by about 50% (Figure 4). Caution must be taken in how we interpret the similarity of these effect sizes; our analysis was based largely on very small plants in individual pots for short time periods, whereas the CNP model test was made in a mature forest ecosystem. The general premise of the hypothesized interaction is well supported in both cases; but there is no *a priori* reason nor expectation that the effect size of the eCO_2 by P interaction would be the same for these two distinct scales. The models were exposed to a common CO_2 manipulation but showed a large variation of the response ratio, whereas in the meta-analysis, the mean is across a range of CO_2 treatments which contributes to the magnitude and the spread of the observed response as documented here.

Moreover, many of these process-based models predicted increased belowground biomass with the extra carbon acquired via photosynthesis to alleviate nutrient stress under eCO_2 (De Kauwe et al., 2014; Fleischer et al., 2019; Jiang et al., 2019b; Zaehle et al., 2014). This assumption corresponds to our H2 hypothesis that the belowground biomass response to eCO_2 would be less affected by LP treatment than that of aboveground biomass. Here, we found no evidence to support this hypothesis.

In fact, our results showed that the extent to which LP limits aboveground and belowground biomass responses to eCO_2 was remarkably similar (Figure 4c). Nonetheless, root length responses did not mirror the belowground biomass responses, suggesting that root morphological responses are likely the responses to alleviate plant nutrient limitation than root biomass responses (Figure 5). A previous synthesis showed a mixture of evidence on biomass eCO_2 responses, with some studies suggesting that nutrient limitation would increase the root response to eCO_2, whilst others showing that the root and shoot responses to eCO_2 would be evenly affected by nutrient limitation (Saxe et al., 1998). Our results clearly contributed to the latter stream of evidence, possibly because of the potting environment that these plants exposed to during experimental manipulation. However, we suggest further investigations are needed to reconcile the apparent discrepancy between different observations to guide more robust model predictions.

In terms of tissue nutrient concentration responses, our results support the model predictions that plant stoichiometric flexibility may be an important mechanism for the positive biomass response to eCO_2 under low P availability (Fleischer et al., 2019). Plants can grow extra biomass under eCO_2 by diluting their tissue nutrient concentrations, as documented here (Figure 2, Figure 4, Figure 6) and elsewhere (Sistla and Schimel, 2012; Hawkesford et al., 2012). The lack of a LP by eCO_2 interaction effect on all tissue nutrient concentrations (Figure 6c) means that the eCO_2-induced tissue nutrient concentration dilution effects were not affected by soil P availability. This result contradicts those CNP models that assume the eCO_2 response is constrained by fixed tissue stoichiometry. Previous model intercomparisons have shown the need for flexible C:N stoichiometry (Zaehle et al., 2014; Medlyn et al., 2015), and we here demonstrated that this also applies to P. However, the degree of stoichiometric variability must be properly constrained. Here, we suggest more data is critically needed to reduce the large variability observed in our data and the relatively small sample sizes to constrain the level of variability.

Our results further showed that the eCO_2 responses of plant nutrient uptake capacity (N_{upt} and P_{upt}) were not affected by LP treatment (Figure 7), which partially contributed to the lack of plant tissue nutrient concentration response to eCO_2 and LP interaction (Figure 6; Figure S9). Given the short

duration of experimental treatment, total plant nutrient content generally reflects total plant nutrient uptake, and there were no statistically significant LP by eCO_2 interactions (Figure S9). Previous field-based CO_2 fertilization studies showed that eCO_2 led to an increased plant N uptake, which then contributed to the positive biomass response to eCO_2 under N limitation (Finzi et al. 2007; Feng et al., 2015). The increased plant N uptake was thought to be the result of increased belowground carbon allocation as well as increased soil organic matter decomposition that led to increased N availability in the soil (Finzi et al., 2007). However, some observations also showed a negative eCO_2 effect on plant N uptake for plants with minimal productivity responses to eCO_2, which was speculated to be partly explained by reduced N supply in the soils (Feng et al., 2015). Nevertheless, it remains unclear whether the lack of CO_2 and LP interaction effects on plant nutrient uptake capacity (Figure 7) and total uptake (Figure S9) in this study would persist over time and in a natural environment, because short-term P manipulations performed under controlled environments may not accurately represent the natural and often long-term feedbacks through which these mechanisms alleviate plant nutrient stresses. Models that incorporated these plant-soil feedbacks generally predicted increased plant nutrient acquisition with eCO_2 (Zaehle et al., 2014; Fleischer et al., 2019). The lack of eCO_2-induced stimulation of nutrient uptake capacity in our meta-analysis therefore suggests the need for more data-driven investigations of the belowground plant-soil interactions (Zaehle et al., 2014; Achat et al., 2016; Fleischer et al., 2019; M. Jiang et al., 2019a).

Roles of vegetation type and mycorrhizal association

Our results that woody plant aboveground biomass responses to eCO_2 were more strongly modulated by LP treatment than those of non-woody plants (Figure 8, Table 2) are generally consistent with the previous analyses that woody plants are more responsive to eCO_2 than non-woody plants (Saxe et al., 1998; Ainsworth and Long, 2004; Ainsworth and Rogers, 2007). The stronger limiting effect of P on woody plant biomass was likely a result of the larger eCO_2 response under HP treatment, which in turn, suggests that woody plants may have more carbon sequestration potential than non-woody plants if P limitation were to be alleviated (Körner, 2006; Norby et al., 2016). Given that woody plants in this study were mostly seedlings, the larger response of woody plants is consistent with the positive

growth feedbacks that young woody plants exhibit during the phase of exponential growth (Norby and Zak, 2011; Kirschbaum and Lambie; 2015; Norby et al. 2016).

In terms of the role of mycorrhizal associations, our results are not consistent with the recent finding that mycorrhizal type is a significant predictor of plant responses to eCO_2 under nutrient limitation (Terrer et al., 2016; Terrer et al., 2019). Our between-group heterogeneity tests consistently showed that mycorrhizal type was not a predictor for plant biomass, photosynthesis, morphology, or tissue nutrient concentration responses to eCO_2 and LP interaction (Table S3; Figure 9a). Instead, our results suggest that the attenuation effects of LP on plant response to eCO_2 were not statistically distinguishable between AM- and ECM-plants (Table S3). The empirical relationships derived by Terrer et al. (2019) showed that soil P availability was significantly correlated with biomass response to eCO_2 in ECM-plants, but not in AM-plants. In our dataset (Figure 1) and those of Terrer et al. (2019), all non-woody plants were classified as AM-plants, whilst woody plants were associated with either AM or ECM. Therefore, it is possible that the test of mycorrhizal effect may have been confounded by different plant growth forms, so we tested this possibility explicitly here. For AM-plants only, which included both woody and non-woody vegetation, we found that plant growth form was a significant predictor for aboveground biomass response to eCO_2 and LP interaction (Figure 9b; Table S4). For woody plants, which included both ECM and AM classifications, we found that mycorrhizal type was not a significant predictor for either aboveground and belowground biomass responses to eCO_2 and LP interaction (Figure 9c; Table S5). Therefore, our results contrast with those of Terrer et al. (2019), and suggest that differences among species in the eCO_2 x LP interaction are more likely due to differences in plant growth form than differences in mycorrhizal associations. However, there are differences between our dataset and that of Terrer et al. (2019). In particular, given the short-term nature of the experiments included in our study, it is possible that mycorrhizal associations were not fully developed and therefore, had a minimal effect in our dataset. More targeted observations are needed to directly evaluate the role of mycorrhizae in modulating plant responses to LP and CO_2 interaction, and reconcile the apparent contradiction between the evidence presented here and in Terrer et al. (2019).

Broad experimental comparisons

Our results that plant biomass responses to eCO_2 were generally limited by low soil P availability are broadly consistent with the evidence presented for the effect of N limitation (Curtis and Wang, 1998; De Graaff, van Groenigen, Six, Hungate and van Kessel, 2006; Liang, Qi, Souza and Luo 2016; Oren et al., 2001; Reich and Hobbie, 2013; Reich et al., 2006). In a meta-analysis including experiments under both low and high N availability, eCO_2-induced increases in plant growth were positive but smaller under low N treatment (De Graaff et al., 2006). In a field-based study comparing eCO_2 responses of loblolly pine grown in soils of different N availabilities (Oren et al., 2001), it was shown that the eCO_2-induced biomass increment was undetectable at the N-impoverished site (open top chamber experiment), but there was some biomass stimulation at the nutritionally-moderate site (DukeFACE). These N by CO_2 experiments generally suggested a strong N limitation effect on plant responses to eCO_2, in agreement with our findings in the meta-analysis on P.

However, it remains unclear whether plants subject to P limitation exhibit a similar temporal response to eCO_2 compared to responses constrained by progressive N limitation (Luo et al., 2004). The mechanisms through which P limitation is imposed on plants are very different from those imposed by N limitation. For example, P can be abundant in soils, but only a tiny fraction of soil P is in the form of labile plant available phosphate (Vitousek et al., 2010; Yang and Post, 2011; Yang, Post, Thornton and Jain, 2013). Plants can increase mineralization and mobilization of the largely unavailable P pool in the soil via increased carbon exudation, phosphatase secretion, carbon trade with mycorrhizal partners, and/or root morphology and growth (Jin et al., 2015). The extent to which these mechanisms affect plant carbon allocation and alleviate plant nutrient stresses under eCO_2 is generally not well quantified, nor are the carbon costs invoked to the plants (Raven, Lambers, Smith and Westoby, 2018). Field CO_2 fertilization experiments performed in a naturally P-deprived forest (EucFACE) showed that eCO_2 did not lead to increased aboveground biomass despite a positive photosynthetic response (Ellsworth et al., 2017; Jiang et al., 2020). In comparison, a nutrient fertilization experiment performed at a comparable, adjacent site showed ~50% increase in stem basal area under ambient CO_2 when additional P was supplied (Crous et al., 2015). While experiments included in this meta-analysis do not fully incorporate the long-term ecosystem-scale feedbacks over

time (Grünzweig and Körner, 2003; Sistla and Schimel, 2012), our results (Figure 4), together with those of Crous et al. (2015), suggest that P by CO_2 interaction would be possible at P-limited EucFACE. Therefore, plant responses to eCO_2 as a function of soil nutrient availability likely depends on the temporal scale of experimental manipulation and observation (Gifford et al. 2000; Körner, 2006; Zavisic and Polle, 2018).

Limitations and future directions

Our meta-analysis of the available scientific literature suggests critical data gaps in capturing the full spectrum of plant responses to eCO_2 and LP interaction. Firstly, experiments included in this study are based entirely on young plants or seedlings grown in constrained soil containers, and mostly under controlled environment. Field-based experiments with longer-term exposure of both CO_2 and P manipulations are critically needed to establish ecosystem-scale understanding beyond the evidence synthesized here. Secondly, our results that root biomass and root morphology showed asynchronous responses to P by CO_2 interaction suggests the morphology or functionality of roots may be more important to study than its biomass response alone. Better assessment of root functionality and its interaction with soil and microbes are therefore needed to improve our mechanistic understanding of plant response to LP and eCO_2 interaction. These experiments are possibly best performed in controlled-environment with plants grown in pots. Thirdly, past studies often focus on plant biomass responses, whilst significantly less data is available on other response variables (Figure 1a). Due to the paucity of data for some response variables, our meta-analyses of the available evidence could be influenced by publication bias and data outliers, as documented in Figure S3 – S8. To provide a more concrete and holistic understanding of the coordinated mechanisms that plants exhibit to cope with P limitation and rising CO_2, we need more studies investigating plant gas exchange, resource use efficiency, root form and functionality, and tissue nutrient concentrations in addition to the continued collection of biomass responses. Last but not least, our results suggest that there was limited data coverage for woody plant responses as compared to those based on non-woody plants, and even less data is available for woody plants associated with AM fungi (Figure 1b). To provide a more balanced assessment of vegetation and mycorrhizal effects in modulating plant responses to eCO_2 and LP interaction, more woody plants and those associated with AM fungi are needed. Taken together, we

recommend further multi-year, field-based experiments focusing on woody plants to fill the critical knowledge gaps in understanding plant responses to eCO_2 under low P.

Conclusions

This meta-analysis provided a quantitative synthesis of the impact of P availability on plant responses to eCO_2 across a range of physiological, biochemical, and morphological variables for young individuals of a range of plant species, with the general aim of addressing a key knowledge gap about P x CO_2 interactions and informing models. We found that low P availability constrains plant photosynthesis, biomass, and leaf area responses to eCO_2. The limitation was stronger in woody plants than non-woody plants, perhaps because young woody plants generally have a larger capacity to respond to eCO_2 when P is non-limiting. Our results were generally consistent across environmentally controlled facilities, including field-based eCO_2 experiments performed in P-deprived soils, indicating that our findings can be an important contribution to develop and evaluate models that predict eCO_2 and P interactions under climate change. More field-based and long-term tests of eCO_2 and P interactions, assessing process-level responses, are needed to further or clarify the interactions observed here.

Competing interests

None declared.

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Data accessibility statement

The dataset can be accessed via: https://doi.org/10.6084/m9.figshare.12612491.v2

The code repository to process the data can be accessed via: https://github.com/mingkaijiang/Meta-analysis-P-by-CO2

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Tables and Figure legends

Table 1. Summary of data included in this meta-analysis. For plant biomass, nitrogen (N) content, phosphorus (P) content, N concentration, P concentration, and tissue N:P ratio, data include those from leaves, stems, roots and whole plant. Leaf gas exchange variables include leaf-level carbon assimilation rate, stomatal conductance, and intrinsic water use efficiency. Morphology variables include leaf area, specific leaf area, leaf mass per area, and root length. Plant nutrient uptake variables include N and P uptake capacity, which were defined as the amount of nutrient taken up per plant or per root mass. Plant nutrient-use efficiency variables include plant N- and P-use efficiency. Number of studies differ from the number of data entries because many studies included a gradient of experimental manipulations.

Table 2. Between-group heterogeneity for the effect of low phosphorus (LP) treatment on woody and non-woody plant responses to elevated CO_2 (eCO_2). Vegetation type (i.e. woody and non-woody) was used as a moderator in the multivariate linear mixed effect model. Results were based on log-transformed response ratios. We tested whether woody and non-woody vegetation responses to eCO_2 under high P treatment (HP) and LP treatment, and the effect of LP on eCO_2 responses were different. Q_M refers to the test of vegetation group effect, with its p-value < 0.05 suggests significant differences between vegetation group. Effect size (%) refers to whether woody and non-woody vegetation response was different (i.e. positive values indicate non-woody > woody response). CI refers to the 95% confidence interval of the effect size. Response variables are: aboveground biomass (AG), belowground biomass (BG), total biomass, leaf nitrogen concentration, root nitrogen concentration, leaf phosphorus concentration, root phosphorus concentration, CO_2 assimilation rate, leaf area, and root length.

Figure 1. Summary of data availability and literature. a) Number of data entries for different response categories, including biomass (i.e. biomass, nitrogen content and phosphorus content of leaf, stem, root and total), concentration (i.e. nitrogen and phosphorus concentrations of leaf, stem, root and total), gas exchange (photosynthesis, and stomatal conductance), morphology (leaf area, root length, leaf mass per area, specific leaf area), nutrient ratio (leaf, stem, root and total N:P ratio),

nutrient uptake capacity (plant N and P uptake capacity), and resource use efficiency (intrinsic water use efficiency, nitrogen use efficiency, and phosphorus use efficiency); and **b)** Number of data entries for different vegetation types (woody and non-woody) and mycorrhizal associations (arbuscular mycorrhizae – AM, and ectomycorrhizae - ECM).

Figure 2. Leaf nitrogen (N) and phosphorus (P) concentration response to elevated CO_2 concentration for woody (green) and non-woody vegetation (yellow), under a) high P and b) low P treatment. Data were extracted from 8 studies, based on 32 paired leaf N and leaf P concentration responses. The dotted lines indicate N:P stoichiometric ratios of 1:16 and 1:20, respectively to indicate the levels of possible P limitation on plants. Leaf N:P ratios above the 1:16 should indicate a predominance of P in plant and hence N limitation, whilst leaf N:P ratios below the 1:20 line should broadly indicate plant P limitation. It is generally thought that the 1:20 line is an indication of plants being limited by P. Arrows indicate the concentrations change from ambient to elevated CO_2. The grey squared box with crossed lines in the inset figures indicate aggregated mean and the aggregated standard error of the CO_2 response curve.

Figure 3. CO_2 and phosphorus (P) treatment effect on plant gas exchange variables. a) The effect of low P (LP) treatment under ambient (aCO_2; grey circle) and elevated CO_2 (eCO_2; black circle), treatment; **b)** the effect of eCO_2 treatment under high P (HP; black diamond) and LP (grey diamond); and **c)** the effect of LP treatment on plant response to eCO_2; black box indicates a positive effect, grey box indicates a negative effect, and a white box indicates a statistically neutral effect. Response variables are: leaf-level photosynthesis (A), stomatal conductance (g_s), and intrinsic water use efficiency (iWUE = A/g_s). Dots and error bars represent means and 95% confidence intervals, respectively, of the log-transformed response ratio estimated based on a random effect model. The effect size was calculated as a percentage response (%). Number of data entries for each variable is denoted as n_e, and number of studies is denoted as n_s, labelled on the right y-axis. We considered the treatment response to be significant ($p < 0.05$) if the confidence interval did not intersect with the black vertical line on each plot (i.e. 0). For the P by CO_2 interaction effect and the P treatment effect,

we considered the LP/HP ratio as a moderator in our mixed-effects model, and then normalized the response to a LP/HP ratio of 0.2.

Figure 4. CO_2 and phosphorus (P) treatment effect on plant biomass variables. a) The effect of low P (LP) treatment under ambient (aCO_2; grey circle) and elevated CO_2 (eCO_2; black circle), treatment; **b)** the effect of eCO_2 treatment under high P (HP; black diamond) and LP (grey diamond); and **c)** the effect of LP treatment on plant response to eCO_2; black box indicates a positive effect, grey box indicates a negative effect, and a white box indicates a statistically neutral effect. Response variables are biomass of aboveground (includes leaf and stem), belowground, and total. Here, plant total biomass constitutes the entire plant, either directly reported by individual studies or summed across major plant organs within the study. Dots and error bars represent means and 95% confidence intervals, respectively, of the log-transformed response ratio estimated based on a random effect model. The effect size was calculated as a percentage response (%). Number of data entries for each variable is denoted as n_e, and number of studies is denoted as n_s, labelled on the right y-axis. We considered the treatment response to be significant ($p < 0.05$) if the confidence interval did not intersect with the black vertical line on each plot (i.e. 0). For the P by CO_2 interaction effect and the P treatment effect, we considered the LP/HP ratio as a moderator in our mixed-effects model, and then normalized the response to a LP/HP ratio of 0.2.

Figure 5. CO_2 and phosphorus (P) treatment effect on plant morphological variables. a) The effect of low P (LP) treatment under ambient (aCO_2; grey circle) and elevated CO_2 (eCO_2; black circle), treatment; **b)** the effect of eCO_2 treatment under high P (HP; black diamond) and LP (grey diamond); and **c)** the effect of LP treatment on plant response to eCO_2; black box indicates a positive effect, grey box indicates a negative effect, and a white box indicates a statistically neutral effect. Response variables are leaf area (LA), leaf mass per area (LMA), and root length (RL). Dots and error bars represent means and 95% confidence intervals, respectively, of the log-transformed response ratio estimated based on a random effect model. The effect size was calculated as a percentage response (%). Number of data entries for each variable is denoted as n_e, and number of studies is denoted as n_s, labelled on the right y-axis. We considered the treatment response to be significant ($p <$

0.05) if the confidence interval did not intersect with the black vertical line on each plot (i.e. 0). For the P by CO_2 interaction effect and the P treatment effect, we considered the LP/HP ratio as a moderator in our mixed-effects model, and then normalized the response to a LP/HP ratio of 0.2.

Figure 6. CO_2 and phosphorus (P) treatment effect on plant tissue nutrient concentration variables. a) The effect of low P (LP) treatment under ambient (aCO_2; grey circle) and elevated CO_2 (eCO_2; black circle), treatment; **b)** the effect of eCO_2 treatment under high P (HP; black diamond) and LP (grey diamond); **c)** the effect of LP treatment on plant response to eCO_2; black box indicates a positive effect, grey box indicates a negative effect, and a white box indicates a statistically neutral effect; and **d-f)** the same as Fig. 3a-c, respectively, but for plant N concentrations. Dots and error bars represent means and 95% confidence intervals, respectively, of the log-transformed response ratio estimated based on a random effect model. The effect size was calculated as a percentage response (%). Number of data entries for each variable is denoted as n_e, and number of studies is denoted as n_s, labelled on the right y-axis. We considered the treatment response to be significant ($p < 0.05$) if the confidence interval did not intersect with the black vertical line on each plot (i.e. 0). For the P by CO_2 interaction effect and the P treatment effect, we considered the LP/HP ratio as a moderator in our mixed-effects model, and then normalized the response to a LP/HP ratio of 0.2.

Figure 7. CO_2 and phosphorus (P) treatment effect on plant nutrient uptake capacity variables. a) The effect of low P (LP) treatment under ambient (aCO_2; grey circle) and elevated CO_2 (eCO_2; black circle), treatment; **b)** the effect of eCO_2 treatment under high P (HP; black diamond) and LP (grey diamond); and **c)** the effect of LP treatment on plant response to eCO_2; black box indicates a positive effect, grey box indicates a negative effect, and a white box indicates a statistically neutral effect. Response variables are, plant nitrogen uptake capacity (N_{upt}), and plant phosphorus uptake capacity (P_{upt}), which were defined as the amount of nutrients taken up per root mass or root length. Dots and error bars represent means and 95% confidence intervals, respectively, of the log-transformed response ratio estimated based on a random effect model. The effect size was calculated as a percentage response (%). Number of data entries for each variable is denoted as n_e, and number of studies is denoted as n_s, labelled on the right y-axis. We considered the treatment response to be

significant ($p < 0.05$) if the confidence interval did not intersect with the black vertical line on each plot (i.e. 0). For the P by CO_2 interaction effect and the P treatment effect, we considered the LP/HP ratio as a moderator in our mixed-effects model, and then normalized the response to a LP/HP ratio of 0.2.

Figure 8. Comparison of woody (WD) and non-woody NWD) plant responses to phosphorus and CO_2 treatments. a & d) the effect of eCO_2 on plant aboveground biomass (AG) and leaf nitrogen concentration (Leaf N) under high phosphorus (HP) treatment, respectively; **b & e)** the effect of eCO_2 on AG and Leaf N under low phosphorus (LP) treatment, and **c & f)** the effect of LP on AG and Leaf N responses to elevated CO_2 (eCO_2), respectively. Dots and error bars represent means and 95% confidence intervals, respectively, of the log-transformed response ratio estimated based on a random effect model. The effect size was calculated as a percentage response (%).

Figure 9. Effect of low phosphorus (LP) treatment on plant responses to CO_2 enrichment (eCO_2) for: a) plants with arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) associations, b) AM plants of woody and non-woody vegetation types, and c) woody plants of AM and ECM associations. Dots and error bars represent means and 95% confidence intervals, respectively, of the log-transformed response ratio estimated based on a random effect model. The effect size was calculated as a percentage response (%). We considered LP/HP ratio as a moderator in our mixed-effects model, and then normalized the response to a LP/HP ratio of 0.2.

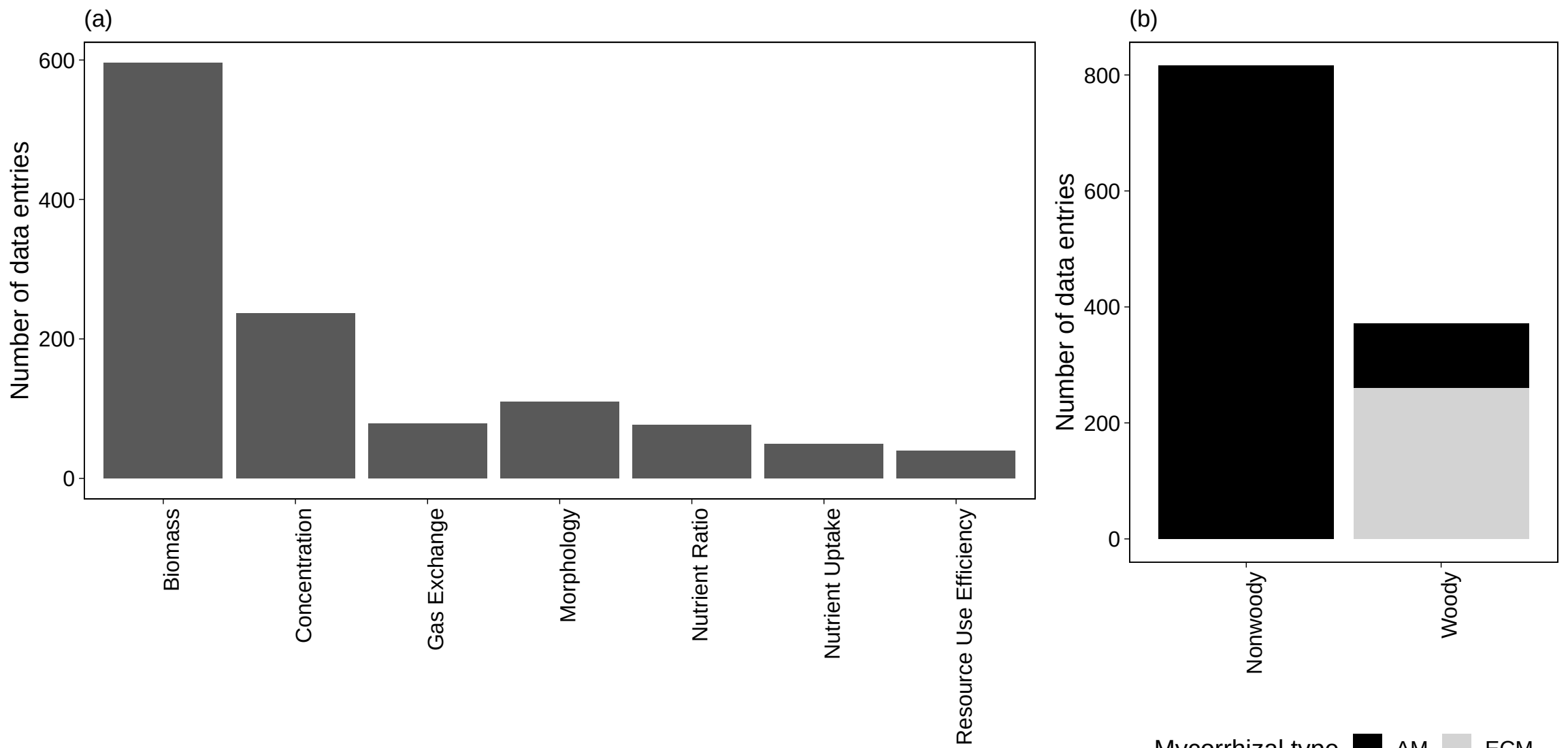
Response variable category	Number of		aCO_2 treatment (μmol mol^{-1})			eCO_2 treatment (μmol mol^{-1})			eCO_2/aCO_2 ratio
	studies (n_s)	data entries (n_e)	low	mean	high	low	mean	high	
Plant biomass	32	204	315	367	400	514	688	1000	1.87
Plant N content	17	85	350	368	400	514	637	800	1.73
Plant P content	25	152	315	367	400	514	684	1000	1.86
Plant N concentration	17	79	350	373	400	514	671	800	1.79
Plant P concentration	26	163	315	368	400	514	692	1000	1.88
Plant tissue N:P ratio	13	70	350	373	400	514	670	800	1.79
Leaf gas exchange	17	96	330	367	400	525	759	1500	2.08
Morphology	17	84	350	373	400	525	716	900	1.92
Plant nutrient uptake capacity	10	48	350	372	400	550	712	935	1.90
Plant nutrient-use efficiency	7	26	350	384	400	652	768	935	2.00

Table 1.

Variable	Sample size (n_e)		CO_2 effect under HP treatment				CO_2 effect under LP treatment				LP effect on eCO_2 response			
	Woody	Non-woody	Q_M	p-value	Effect size (%)	CI (%)	Q_M	p-value	Effect size (%)	CI (%)	Q_M	p-value	Effect size (%)	CI (%)
CO_2 assim. rate	38	15	0.71	> 0.05	-13.2	-37.5 to 20.5	0.75	> 0.05	-11.5	-32.9 to 16.8	1.45	> 0.05	-6.9	-17.2 to 4.6
Leaf area	10	16	3.21	> 0.05	-9.9	-19.5 to 1.0	2.05	> 0.05	-18.3	-38.0 to 7.7	1.49	> 0.05	-10.1	-24.3 to 6.7
Root length	6	20	0.03	> 0.05	-2.9	-30.4 to 35.3	0.77	> 0.05	8.9	-10.0 to 31.7	2.53	> 0.05	-23.1	-44.4 to 6.3
AG biomass	49	98	6.11	**0.01**	-14.7	-24.9 to -3.2	4.72	**0.03**	-13.4	-24.0 to -1.4	10.02	**< 0.01**	-22.2	-33.4 to -9.1
BG biomass	19	51	0.12	> 0.05	4.6	-18.8 to 34.8	0.36	> 0.05	8.2	-16.4 to 40.0	1.77	> 0.05	-17.1	-37.0 to 9.2
Total biomass	35	49	0.85	> 0.05	10.0	-10.2 to 34.7	0.59	> 0.05	8.3	-11.7 to 32.8	0.06	> 0.05	-2.4	-20.2 to 19.3
Leaf N conc.	10	24	4.98	**0.02**	-21.2	-36.1 to -2.9	4.43	**0.04**	-25.2	-42.9 to -2.0	5.10	**0.02**	-15.1	-26.3 to -2.1
Root N conc.	4	13	0.47	> 0.05	24.8	-33.5 to 134.0	0.30	> 0.05	18.8	-36.1 to 120.9	0.02	> 0.05	6.6	-52.2 to 137.5
Leaf P conc.	32	45	0.09	> 0.05	-2.1	-15.4 to 13.2	0.98	> 0.05	-7.8	-21.5 to 8.3	0.16	> 0.05	-4.5	-23.8 to 19.6
Root P conc.	13	21	0.50	> 0.05	-9.5	-31.5 to	0.08	> 0.05	-3.4	-23.5 to	0.01	> 0.05	-2.3	-34.5 to

	19.5	22.0	45.8

Table 2.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Concentration
Gas Exchange
Morphology
Nutrient Ratio
Nutrient Uptake
Resource Use Efficiency
(b)
Number of data entries
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600
400
200
0
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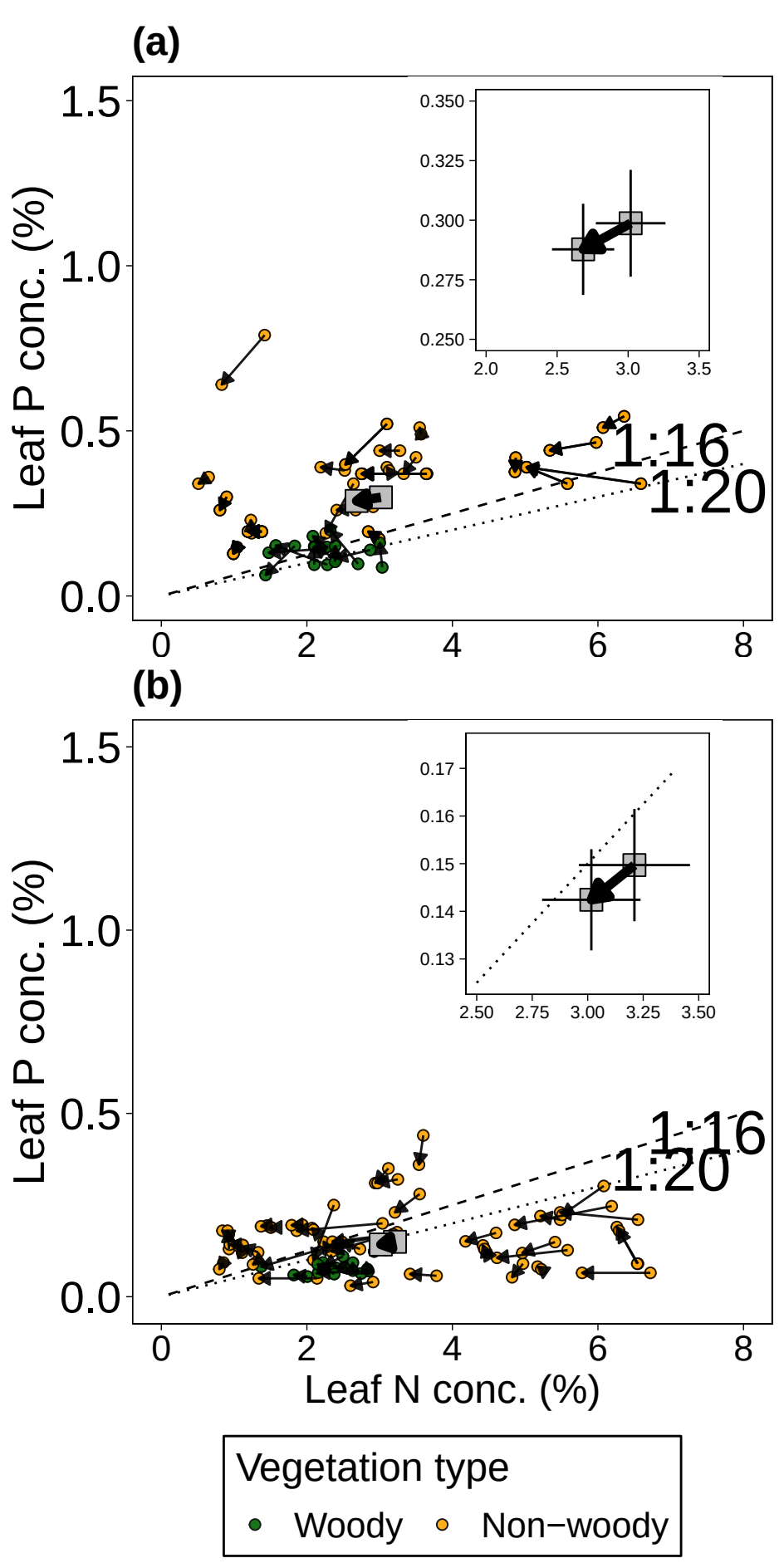
Woody
Mycorrhizal type
AM
ECM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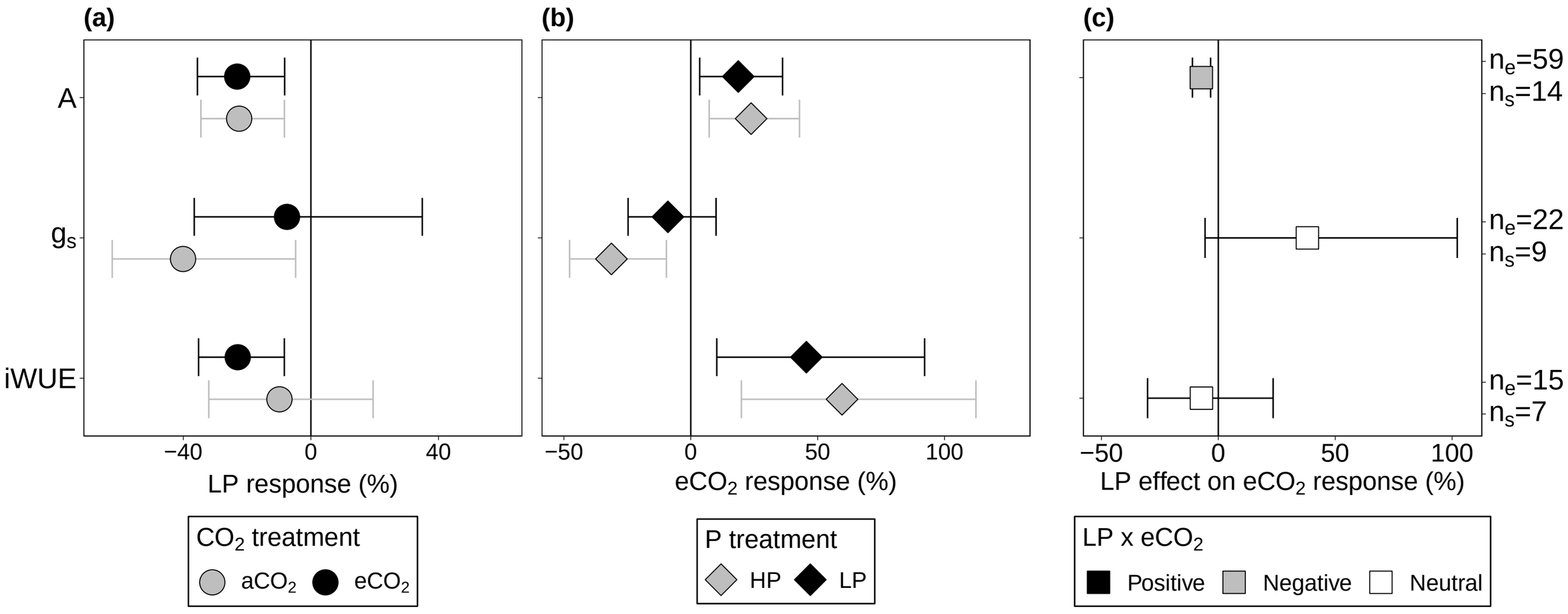
0.300
0.275
0.250
2.0
2.5
3.0
3.5
1:16
1:20
0
2
4
6
8
(b)
Leaf P conc. (%)
1.5
1.0
0.5
0.0
0.17
0.16
0.15
0.14
0.13
2.50
2.75
3.00
3.25
3.50
1:16
1:20
0
2
4
6
8
Leaf N conc. (%)
Vegetation type
Woody
Non−woody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(b)
(c)
A
gs
iWUE
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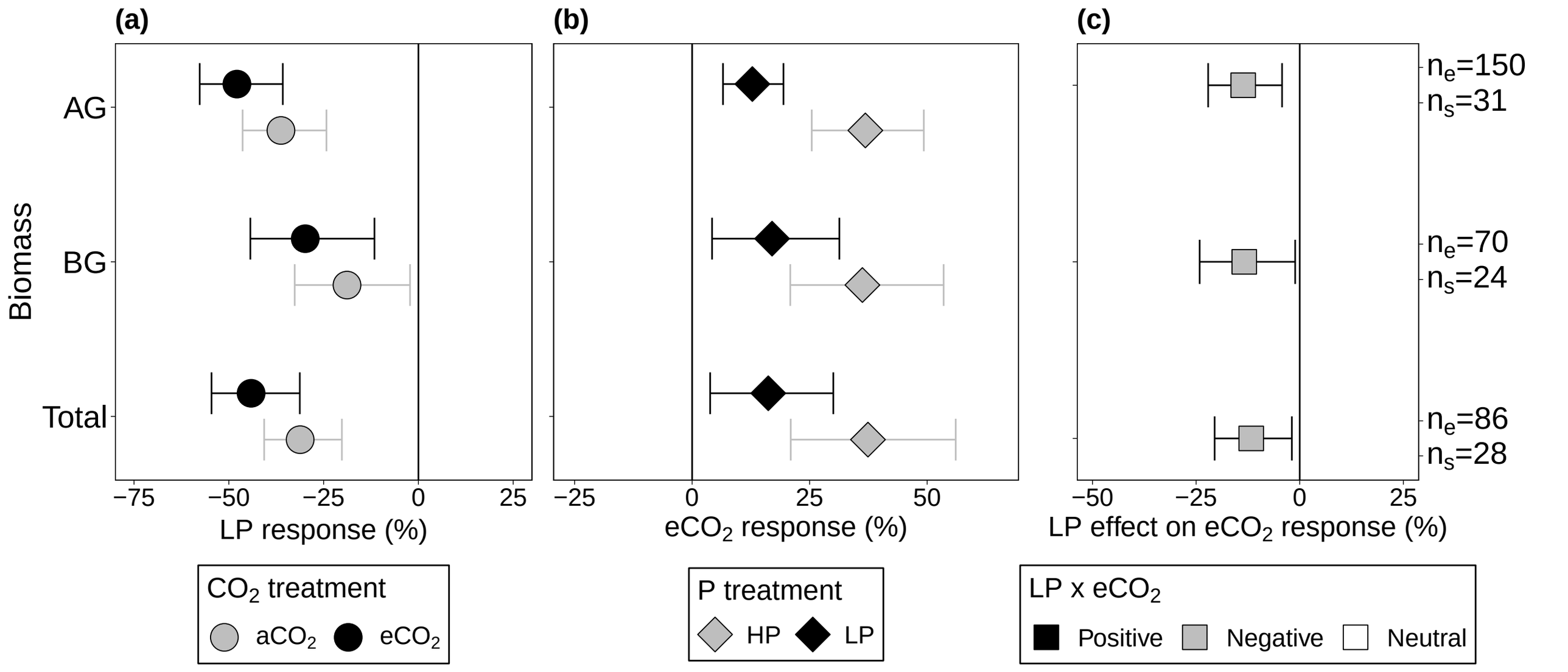
0
50
100
eCO2 response (%)
ne=59
ns=14
ne=22
ns=9
ne=15
ns=7
−50
0
50
100
LP effect on eCO2 response (%)
CO2 treatment
aCO2
eCO2
P treatment
HP
LP
LP x eCO2
Positive
Negative
Neutral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(b)
(c)
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25
50
eCO2 response (%)
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−25
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25
LP effect on eCO2 response (%)
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ns=31
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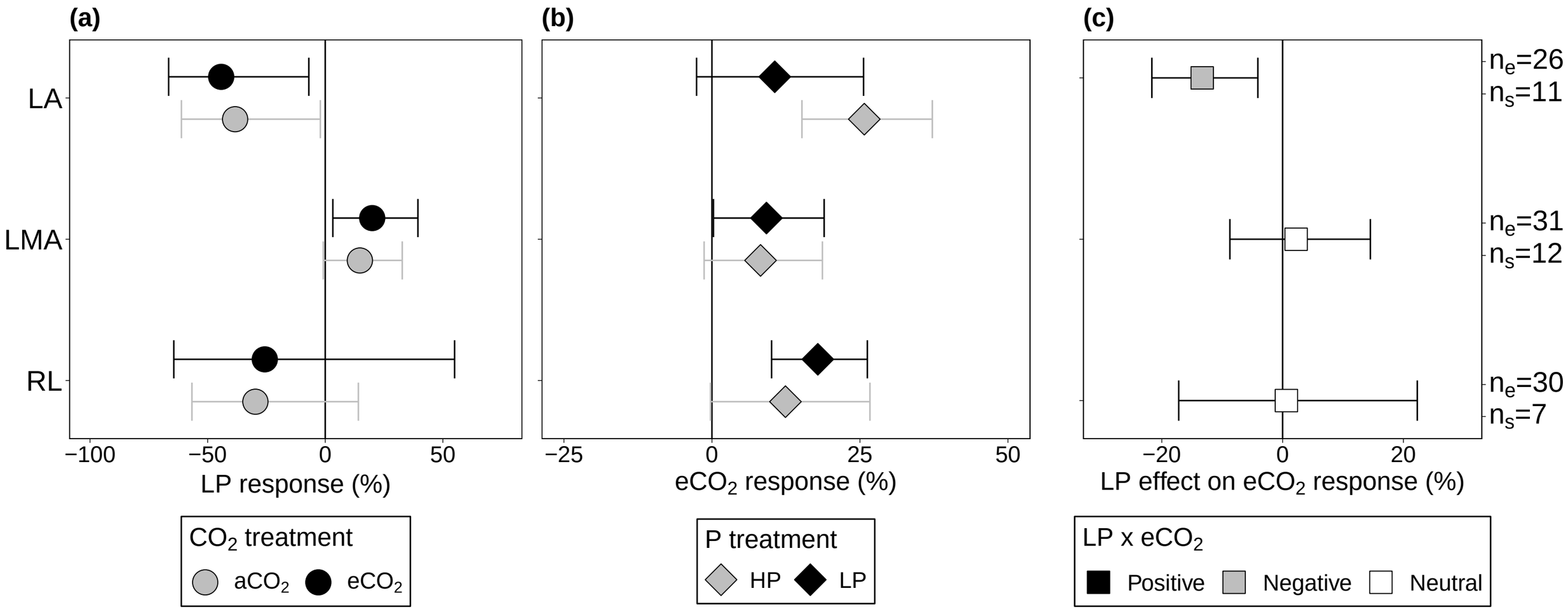
eCO2
P treatment
HP
LP
LP x eCO2
Positive
Negative
Neutral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(b)
(c)
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ns=11
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ns=7
CO2 treatment
aCO2
eCO2
P treatment
HP
LP
LP x eCO2
Positive
Negative
Neutral

(a)
(b)
(c)
(d)
(e)
(f)
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N concentration
Leaf
Stem
Root
Total
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n_e=16
n_s=6
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LP response (%)
−60 −40 −20 0 20 40
eCO_2 response (%)
−40 −20 0 20 40 60
LP effect on eCO_2 response (%)
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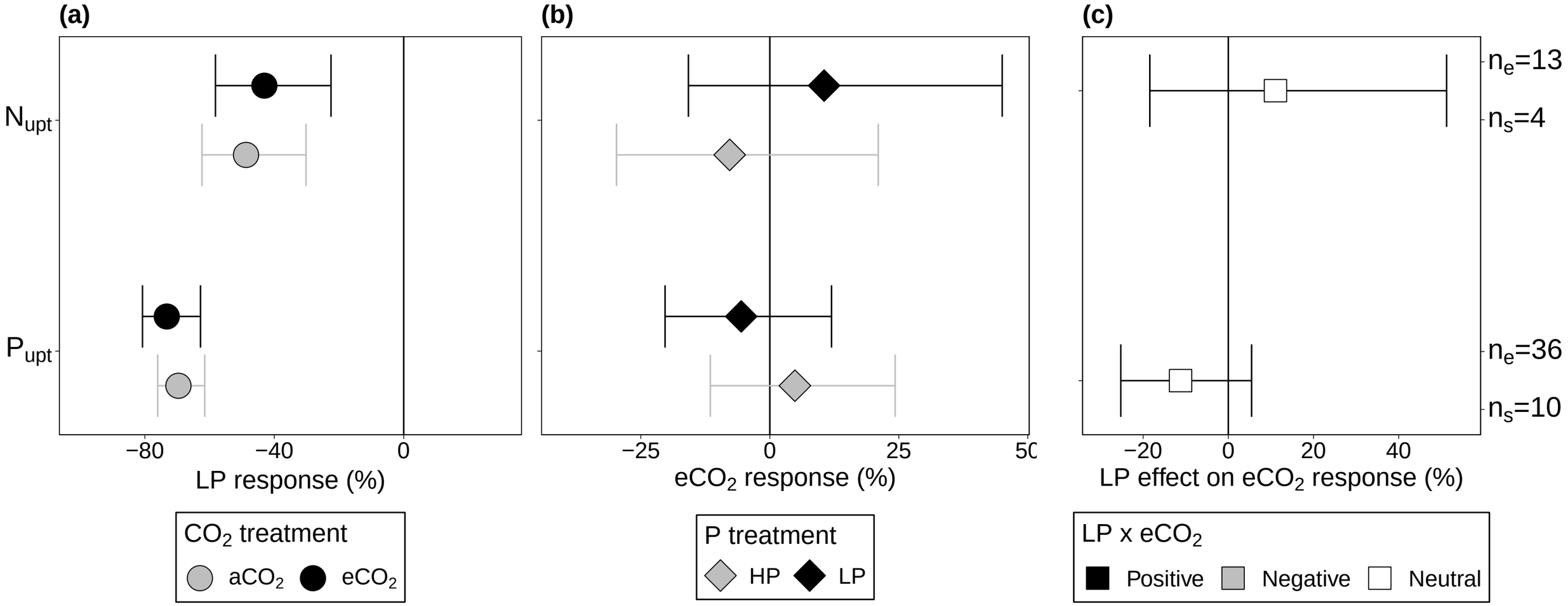
aCO_2
eCO_2
P treatment
HP
LP
LP x eCO_2
Positive
Negative
Neutral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20
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LP effect on eCO_2 response (%)
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n_s=4
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CO_2 treatment
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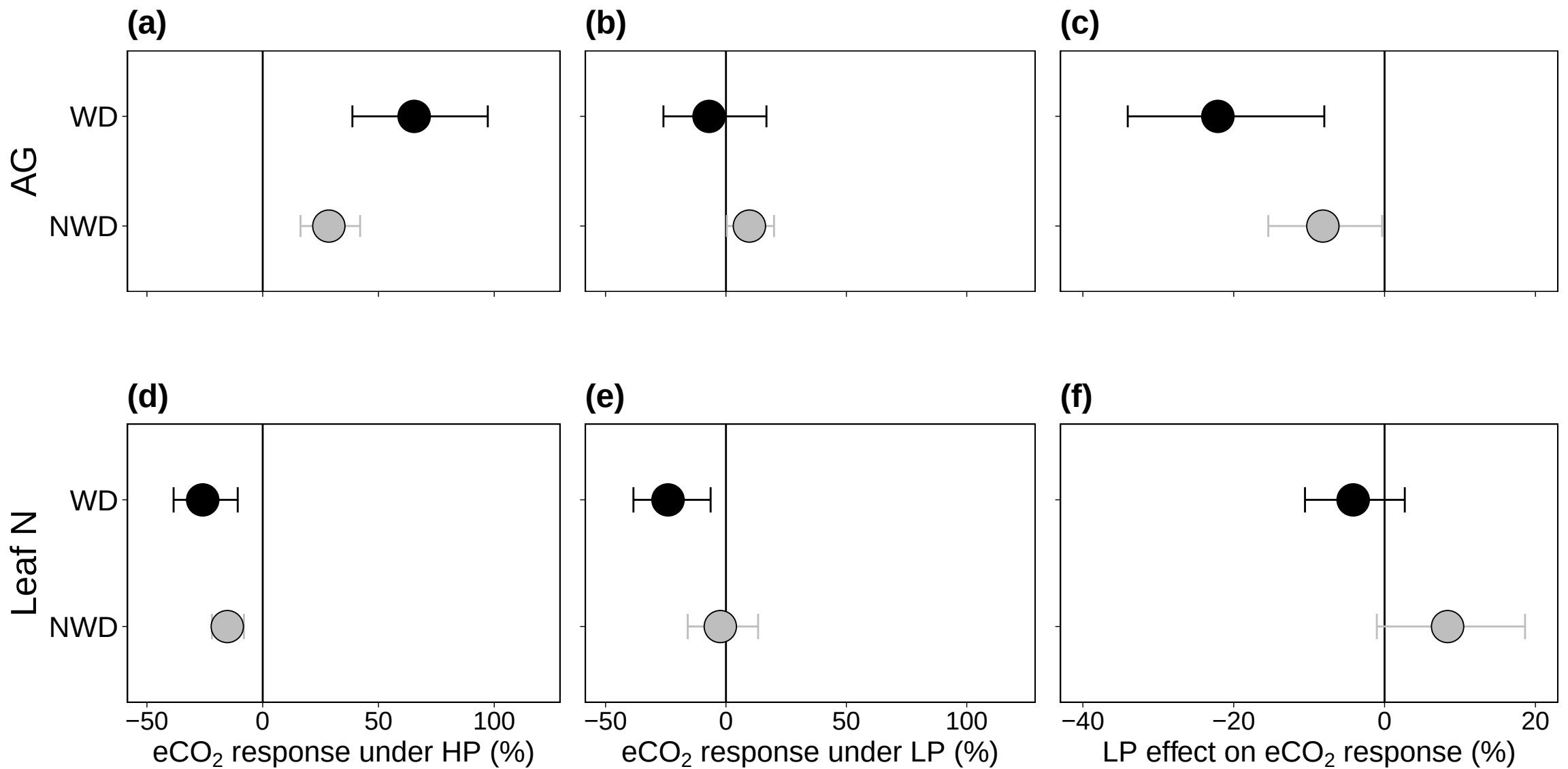
eCO_2
P treatment
HP
LP
LP x eCO_2
Positive
Negative
Neutral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Leaf N
WD
NWD
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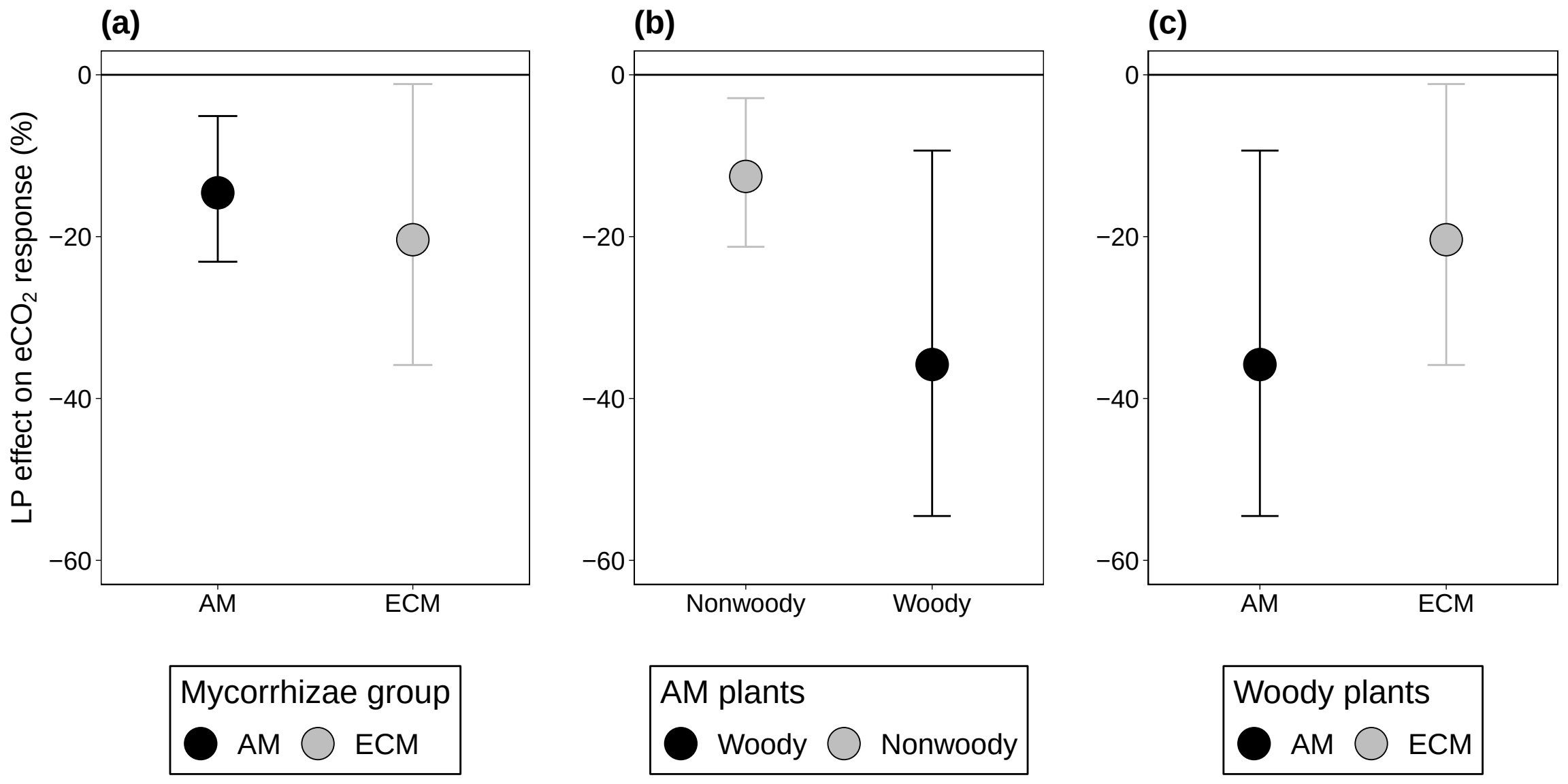
0
50
100
−40
−20
20
eCO2 response under HP (%)
eCO2 response under LP (%)
LP effect on eCO2 response (%)


(a)
(b)
(c)
LP effect on eCO2 response (%)
0
−20
−40
−60
AM
ECM
Nonwoody
Woody
Mycorrhizae group
AM
ECM
AM plants
Woody
Nonwoody
Woody plants
AM
ECM